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ADAPTABILITY OF WHITE JABON (*Anthocephalus cadamba* Miq.) SEEDLING FROM 12 POPULATIONS TO DROUGHT AND WATERLOGGING

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ABSTRACT

The study was carried out for investigation of the adaptability of white jabon seedlings from 12 populations to drought and water logging stresses in a controlled green house. The results showed that the adaptive responses of white jabon seedling to drought and waterlogging stresses were affected by genotype (population). The drought and waterlogging stresses significantly inhibited plant growth, biomass accumulation and allocation, leaf area, also decreased chlorophyll content, increased carotenoids contents, and accumulated free proline. Relative water content and specific leaf area tended to be higher in waterlogging and declined in drought stresses. The result clearly indicated that white jabon seedlings were more adaptive to waterlogging than to drought stresses. Moreover, there were different responses to drought and waterlogging stresses between the twelve populations. Kampar, Gowa, Kuala Kencana and OKI populations exhibited higher growth performance and stress tolerance index to be adapted to waterlogging stress, while Gowa, Pomalaa and Kampar populations had relatively better growth performance in the drought stress.

Keywords: *Anthocephalus cadamba,* genotype, growth, population, stress tolerance index

INTRODUCTION

White jabon [*Anthocephalus cadamba* (Roxb.) Miq., family Rubiaceae] is a fast-growing tree species that is native to Indonesia. It can be used for many purposes, such as the timber for pulp, plywood and light construction (Soerianegara and Lemmens, 1993), and various parts of the plant have bioactive compounds, including antioxidant, hypoglycemic, hypo-lipidemic, antibacterial and antimicrobial properties (Acharyya *et al*., 2011; Mishra and Siddique, 2011). This species grows widely in the tropical evergreen lowland rain forests of Asia, which extend through India, Nepal, Burma, Sri Lanka and Malaysia and across Indonesia, Philippines and New Guinea (Lamprecht, 1989). In Indonesia, the species is distributed on almost all islands and it plays an important role in both commercial and traditional farming systems in several areas of the country (Kallio *et al*., 2011; Irawan and Purwanto, 2014).

At present, white jabon is extensively planted in many types of sites, such as in wet and dry lands (Haneda *et al.,* 2012), without considering of suitability of seed sources or populations, and in particular, so many planting activities are threatened by failure. Drought and water logging limit the potential range of many species by affecting seedling survival, growth and development potential of plants. They show significant effects in the initial stages of plant growth (e.g. during the first year of cultivation) (Kozlowski, 1997; Dunisch *et al*., 2003) and endanger plant survival. Some studies related to white jabon adaptations to water stresses showed that the species was not suitable for critical land rehabilitation (Voukko and Otsamo, 1996), not optimal growth at low soil field capacity

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(Soetrisno, 1996) and also in shallow water table soil (Mansur and Suharman, 2011).

Drought and waterlogging stresses in several Indonesian areas were predicted to increase due to climate change (Policy Synthetic Team, 2008) and it is potential to increase an adverse effect to initial seedling growth and succes of forest and land rehabilitation activities. To promote the successful curent-year tree seedlings settlement, especially in waterloogging and drought land, the key to understand is how they are adapted to drought and waterlogging, a critical condition for silviculture activities of white jabon. However, very little of knowledge is known about inter-population variation in adaptability to the stresses in white jabon. Assessment of populationsfrom several geography ranges is important to select the adapted genotype to drought and waterlogging stresses, because some studies reported that several populations naturally often found in the transitional zone between swampy, permanently flooded areas and periodically flooded areas and it is also found in drier areas with low annual rainfalls (Soerianegara and Lemmens, 1993). Comprehensive knowledge about provenance responses on drought and waterlogging can become a reference in development of seed transfer guideline (Wang *et al*., 1989), selection of adaptive provenances, and also as a key of adaptation strategy on climate change (Millar *et al.,* 2007). The objective of this study was to investigate the adaptability of white jabon seedlings from the twelve populations to drought and water logging stresses in a controlled greenhouse.

MATERIALS AND METHODS

Sample Collection

White jabon seeds were collected from 12 populations distributed in 7 islands in Indonesia (Figure 1, Table 1). The seeds were collected from 10 - 20 dominant trees per population and a minimum distance of 50 m on average was maintained between each seed tree to prevent sampling trees from the same parent or pedigree. The seeds from individual trees were equally sampled by weight and bulked by population for the experiment.

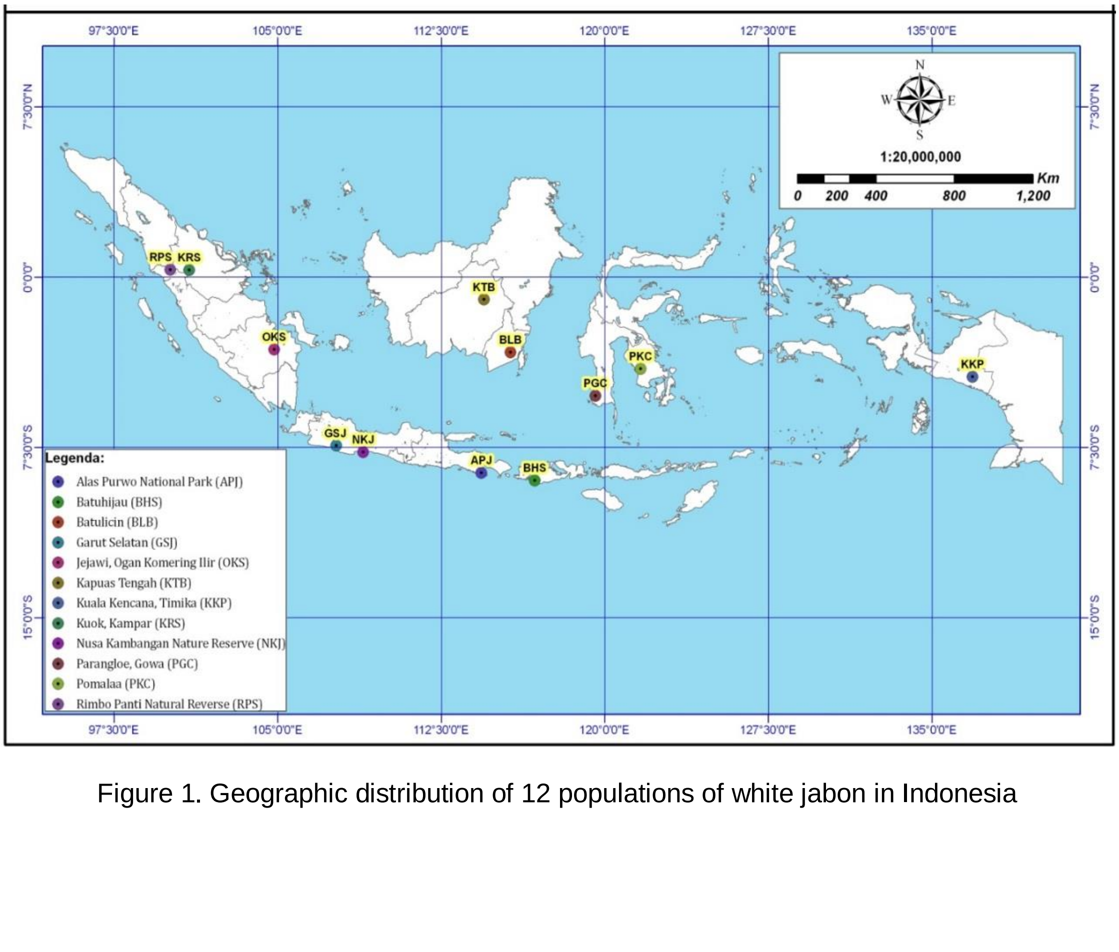

Figure 1. Geographic distribution of 12 populations of white jabon in Indonesia

Table 1.Geographic origin of the investigated population

No.	Locations	Abbreviation	Island	Latitude	Longitude	Altitude (m asl)	Climate type (Schmidt and Fergusson)
1.	Rimbo Panti Nature Preserve	RPS	Sumatra	00°19' U	100°05' E	294	A
2.	Kuok, Kampar, Riau	KRS	Sumatra	00°18' U	100°57' E	50	A
3.	Jejawi, Ogan Komering Ilir (OKI)	OKS	Sumatra	03°12' S	104°51' E	23	B
4.	Garut Selatan	GSJ	Java	07°26' S	107°42' E	628	B
5.	Nusa Kambangan Nature Preserve	NKJ	Nusa Kambangan	07°43' S	108°55' E	40	D
6.	Alas Purwo National Park	APJ	Java	08°38' S	114°21' E	33	D-E
7.	Kapuas Tengah	KTB	Borneo	01°00' S	114°28' E	147	B
8.	Batu Licin	BLB	Borneo	03°19' S	115°41' E	47	A
9.	Pomalaa	PKC	Celebes	04°03' S	121°39' E	210	C
10.	Parangloe, Gowa	PGC	Celebes	05°14' S	119°35' E	119	C
11.	Batu Hijau	BHS	Sumbawa	08°58' S	116°48' E	53	D
12.	Kuala Kencana	KKP	Papua	04°24' S	136°52' T	107	A

Seedling Preparation and Experimental Design

White jabon seedlings were tested in a controlled condition in the green house to identify their adaptability on different water stress conditions. For each population, 10 normal seedlings (± 3 cm in height) are randomly taken from sowing boxes and planted in pots (18.5 cm in diameter x 16 cm in height). There were 40 pots planted by seedling for each population. On the early stage of growing, seedlings were placed in an optimal condition in nursery. After 2 months, the seedlings were moved to the greenhouse. During the experiment, the average day and night temperatures in the greenhouse were 34°C and 29°C, respectively, and the relative humidity ranged from 60 to 75%. The treatments of water stress condition were done after 1 month seedling in the green house.

A completely randomized design was used with factorial combinations of water stress [well-water supply (control), 3-5 cm-water logging (W_L), watered every 2 days with 50% field capacity (W_{50}) and 25% field capacity (W_{25})] and white jabon populations (12 populations). A pot was the experimental unit and each treatment was replicated 10 times; thus, there were a total of 40 seedlings per populations. The soil volumetric water content for control and drought treatments was maintained at 32.8 ± 2.8%, 25.3 ± 0.7%, and 19.8 ± 1.4% for the control, W_{50}, and W_{25} treatments, respectively. 120 days after the beginning of the treatment, the experiment was terminated.

Measurement of Seedling Growth Characteristics and Biomass Production

Height and root collar diameter of seedlings were recorded at prior to the experiment and at the end of the experiment. The growth of height and diameter was resulted from reduction of the final measurement with the first measurement. At the end of the drought and water logging regime, all plants were measured for leaf area, number of leaf, biomass, root length, adventitious roots and lenticels. For biomass measurements, all plants were harvested and divided into roots, stems and leaves. Roots, stems and leaves were dried separately in a drying oven at 70°C for 48 h and weighed to ±0.0001 g. Leaves and stems were aggregated and are subsequently referred to as above-ground biomass and roots are referred to as below-ground biomass. Total biomass is the sum of above-ground and below-ground biomass. Root-shoot ratio and specific leaf area was calculated using the following formula Li *et al*. (2011).

Measurement of Relative Water Content, Stomatal Density and Leaf Thickness

Three seedlings were randomly selected and then three leaves per seedling were sampled for relative water content, stomatal density and leaf thickness measurements. Relative water content was determined gravimetrically on the selected leaves from the mid-canopy position following method of Li *et al*. (2011). Stomatal density was measured using a nail polish impression of the abaxial surface of the first fully developed leaf harvested at the end of the treatments and counted under a light microscope in three random fields per leaf at ×40 magnification. For leaf thickness measurements, three slides were prepared for each leaf. A cryotome was used to cut cross-sections that were adhered to slides. Digital images were taken of each slide at x40 magnification with a digital still camera in conjunction with a microscope (Olympus L15643).

Analysis of Pigments and Proline Contents

The concentrations of chlorophyll A, chlorophyll B, total chlorophyll, carotenoids, and proline were measured from a single leaf at the second pair from the apices of the three randomly seedlings. The total chlorophyll and carotenoids were determined using the method described by Lichtenthaler (1987) using a Shimadzu UV-1201 spectrophotometer, while the free proline content was measured according to the method of Bates *et al*. (1973) using Hitachi U-3900H spectrophotometer.

Statistical Analysis

The data were analyzed with ANOVA to test the effect on the water stress and populations on the seedling morphological, anatomical and physiological variables. Duncan's multiple range test at a significance level $p<0.05$ was used to compare significant differences in the means. The statistical analysis was performed employing SAS 9.1 for windows. Stress tolerance index was analyzed on the growth parameters (height, diameter and total biomass) using formula of Fernandez (1992). Principal component analysis was used to explain the pattern of adaptation variation among the populations based on seedling morphological characteristics.

RESULT AND DISCUSSION

Growth Characteristics and Biomass Production

Drought stresses caused significant growth decline in seedling height, root collar diameter, above-ground biomass, below-ground biomass, total biomass, root length and leaf area of white jabon seedlings, except of root shoot ratio, showing the significant increase on drought stress (Table 2). Similar results of drought responses on the growth characteristics have been reported in several previous studies (Yang and Miao, 2010; Ky-Dembele *et al*., 2010). Water deficits reduce the number of leaves per plant, and individual leaf size, and leaf longevity by decreasing the soil's water potential. Generally, when water availability is limited, the root-shoot ratio of plants increases because roots become less sensitive than shoots to growth inhibitor that is low water potentials (Li *et al*., 2011).

In waterlogging stress, height, biomass accumulations, root length and leaf area also were reduced compared to the control. On the contrary, the root-shoot ratio and root collar diameter in the waterlogging treatment were higher than in the other treatments. The similar result also occurred in waterlogged seedlings of *Carex lasiocarpa* and *C. limosa* (Lu, 2011). According to Kozlowski (1997), waterlogging often affects xylem and phloem production. Waterlogged soils increased stem diameter growth more as a result of increasing bark thickening and stem hypertrophy, which then cause xylem increment. The increase in bark thickness was associated with accelerated proliferation of phloem parenchyma cells and large amounts of intercellular space in the phloem (Yamamoto and Kozlowski, 1987).

In comparison among populations, Kampar population showed the best seedling height, root collar diameter and total biomass in the W_L treatment, while in the drought stress (W_{50} and W_{25}), Gowa population had the highest seedling height and root collar diameter. For total seedling biomass, Batu Hijau population was the highest in the moderate drought (W_{50}) and Gowa population had the highest total biomass in the severe drought (W_{25}). The Kapuas population had lowest seedling height and root collar diameter in all treatments. There was no seedling died in the control and W_L treatments, while in the W_{50} treatment, one seedling from Batu Licin population, and three seedlings from Kapuas population were observed to die at the end of the experiment. In the W_{25} treatment, dead seedlings increased, covering six seedlings from Kapuas population, three seedlings from Batu Licin and Rimbo Panti populations, and one seedling from Garut, Alas Purwo, and Kuala Kencana populations. The growth status and survival rate under drought and waterlogging stress can be regarded as one of important indexes in plant tolerance (Mommer *et al*., 2006).

Waterlogging stress also emerged adventives root and hypertrophied lenticels that were not found in other treatments. The production of adventives root and lenticels on the submerged portions of stems in waterlogged seedlings has been described as a morphologically adaptive mechanism against the waterlogged sites (Yamamoto *et al*., 1995; Glenz *et al*., 2006) to increase the uptake of O_2 by aerial tissues and promotes its transport into the root system (Konzlowski, 1997; Glens *et al*., 2006). The adventives root is very important for plants under root hypoxia or anoxia to obtain oxygen from the environment because it may directly get oxygen from the surroundings and internally transport oxygen through aerenchyma. Furthermore, the ability to produce adventives root is commonly associated with enhanced tolerance to waterlogging (Steffens *et al*., 2006). Kampar population had more amounts of adventives root and lenticels than the other populations indicating the population that is more adaptive to waterlogged sites.

Table 2. Seedling height, root collar diameter, biomass accumulation, root-stem ratio, root length, number of leaf and leaf area of white jabon seedling under four water treatments

Population	Treatment	SH (cm)	RCD (mm)	AGB (g)	BGB (g)	TB (g)	R:S ratio	RL (cm)	NL	LA (cm^2)
Rimbo Panti	Control	26.1 a-d	2.7 e-g	8.0 a-c	5.8 a	13.8 a	0.63 k-o	51.8	5.8 b-f	114.68 d-f
	W_L	18.2 h-i	3.4 b-f	7.1 b-d	3.8 d-g	11.0 b-e	0.54 o	45.6	4.9 c-j	85.29 g-k
	W_{50}	9.3 j-n	1.2 i-l	1.3 h-j	2.3 h-l	3.6 g-k	1.69 a	48.2	3.9 h-p	62.61 l-q
	W_{25}	4.6 o-r	0.8 l	1.1 h-j	1.9 j-n	3.1 g-k	1.63 a-d	26.0	2.6 o-q	44.11 q-s
Kampar	Control	27.7 ab	3.1 c-h	9.1 a	5.5 ab	14.6 a	0.63 l-o	51.9	4.9 c-j	146.11 Ab
	W_L	23.2 d-g	4.5 a	8.5 ab	5.0 a-d	13.5 ab	0.59 m-o	41.7	4.4 f-m	120.43 c-e
	W_{50}	5.5 m-r	1.4 i-l	1.5 h-j	2.4 h-l	3.9 g-j	1.59 a-e	48.6	4.6 e-k	94.02 f-i
	W_{25}	4.7 n-r	0.9 kl	1.2 h-j	1.7 i-o	3.0 g-k	1.42 a-g	35.1	2.9 m-q	50.23 o-s
OKI	Control	29.5 ab	3.6 a-e	8.2 ab	5.6 ab	13.9 a	0.69 k-o	53.5	4.7 d-k	151.63 Ab
	W_L	19.4 g-i	3.7 a-e	8.1 a-c	4.7 a-e	13.0 a-c	0.58 m-o	33.0	6.9 ab	91.88 g-j
	W_{50}	6.9 m-r	1.3 i-l	1.9 g-j	1.8 i-o	3.8 g-j	0.96 g-o	50.4	3.8 h-p	70.85 j-o
	W_{25}	3.4 p-r	1.2 i-h	0.7 ij	0.9 l-o	1.7 h-k	1.32 a-g	31.7	2.9 m-q	29.18 st
Garut	Control	19.4 g-i	3.6 a-e	8.7 ab	5.7 a	14.5 a	0.65 l-o	62.0	4.3 f-m	159.90 a
	W_L	12.3 j	2.9 d-h	6.2 d-f	4.3 b-f	10.5 c-f	0.68 k-o	38.0	3.6 h-q	99.83 f-g
	W_{50}	5.8 l-r	1.0 kl	2.0 g-j	2.2 i-m	4.2 g-i	1.12 c-m	40.0	3.0 l-q	75.22 i-m
	W_{25}	2.9 qr	0.8 l	1.1 h-j	1.8 i-o	3.0 g-k	1.65 ab	37.8	2.6 o-q	43.75 q-s

Table 2. *(Continued)*

Population	Treatment	SH (cm)	RCD (mm)	AGB (g)	BGB (g)	TB (g)	R:S ratio	RL (cm)	NL	LA (cm^2)
Nusa Kambangan	Control	24.5 c-f	3.7 a-e	5.5 ef	3.8 d-g	9.3 ef	0.69 k-o	48.6	4.4 f-m	136.75 bc
	W_L	20.5 f-i	4.1 a-c	4.8 f	3.2 f-i	8.0 f	0.64 l-o	25.9	5.1 c-h	98.04 f-h
	W_{50}	9.1 j-o	1.4 i-l	1.4 h-j	2.0 i-n	3.4 g-k	1.43 a-g	41.0	3.4 j-q	83.28 h-l
	W_{25}	3.8 p-r	1.0 kl	1.3 h-j	1.6 i-o	3.0 g-k	1.35 a-g	29.8	3.0 l-q	45.17 p-s
Alas Purwo	Control	22.8 d-g	2.8 e-h	5.6 e-f	3.9 c-g	9.5 ef	0.71 k-o	36.9	4.0 g-o	105.93 ef
	W_L	9.9 j-l	3.9 a-d	3.2 g	1.6 i-o	4.9 g	0.52 o	22.6	5.0 c-i	73.21 i-n
	W_{50}	5.1 m-r	1.1 j-l	1.3 h-j	1.6 i-o	2.9 g-k	1.10 d-m	21.9	4.1 g-n	48.58 p-s
	W_{25}	2.9 qr	0.6 l	1.0 h-j	1.5 j-o	2.6 g-k	1.51 a-f	28.7	2.9 m-q	35.16 r-t
Kapuas	Control	10.6 jk	2.2 g-j	2.7 gh	1.8 i-o	4.4 gh	0.68 k-o	37.2	5.0 c-i	88.67 g-j
	W_L	7.6 k-q	3.7 a-e	2.3 h-i	1.3 j-o	3.6 g-k	0.56 no	29.7	5.5 c-g	52.95 n-r
	W_{50}	3.1 qr	1.0 kl	1.2 ij	0.7 m-o	1.4 i-k	1.10 e-n	27.2	3.5 i-q	54.82 m-r
	W_{25}	2.6 r	0.7 l	0.6 j	0.6 n-o	1.1 jk	1.01 f-o	13.0	2.7 n-q	32.71 r-t
Batu Licin	Control	9.6 j-m	2.1 h-k	2.6 gh	1.7 i-o	4.2 g-i	0.65 l-o	42.6	6.0 b-e	82.07 h-l
	W_L	7.1 k-r	3.3 b-g	2.0 g-j	1.2 k-o	3.2 g-k	0.63 l-o	26.8	6.0 b-e	46.79 p-s
	W_{50}	3.3 p-r	0.8 l	0.7 ij	0.6 n-o	1.4 i-k	0.89 h-o	17.7	3.5 i-q	40.52 q-s
	W_{25}	2.6 r	0.7 l	0.4 i	0.4 o	0.8 k	0.98 f-o	15.0	2.5 o-q	17.01 t
Gowa	Control	25.7 a-e	4.0 a-d	8.3 ab	5.4 ab	13.7 ab	0.67 l-o	47.7	5.8 b-d	144.70 ab
	W_L	21.7 e-i	4.7 a	7.6 a-d	5.0 a-d	12.9 a-d	0.67 l-o	34.3	8.0 a	105.59 e-g
	W_{50}	9.6 j-n	2.2 g-j	2.0 g-j	2.5 h-k	4.5 gh	1.26 a-g	40.8	4.5 e-l	88.12 g-j
	W_{25}	7.9 k-p	1.2 i-l	1.6 g-j	2.0 i-n	3.7 g-k	1.26 a-g	41.9	2.8 n-q	43.04 q-s
Pomalaa	Control	21.8 e-i	3.8 a-e	7.9 a-d	6.1 a	14.0 a	0.79 i-o	55.3	6.7 ab	131.28 b-d
	W_L	17.8 i	3.6 a-e	7.5 a-d	5.8 a	13.3 ab	0.73 j-o	38.0	6.2 bc	99.47 f-g
	W_{50}	6.8 k-r	1.6 i-l	1.7 g-j	2.0 i-n	3.7 g-k	1.24 a-g	53.9	3.2 k-q	73.05 i-n
	W_{25}	4.5 o-r	1.0 kl	1.2 h-j	1.9 i-n	3.0 g-k	1.64 a-c	33.3	2.7 n-q	41.85 q-s

Table 2. *(Continued)*

Population	Treatment	SH (cm)	RCD (mm)	AGB (g)	BGB (g)	TB (g)	R:S ratio	RL (cm)	NL	LA (cm^2)
Batu Hijau	Control	20.8 f-i	3.7 a-e	8.7 ab	5.8 a	14.6 a	0.67 l-o	53.0	6.1 b-d	124.22 c-e
	W_L	19.7 g-i	4.0 a-d	7.5 a-d	4.7 a-e	12.2 a-d	0.65 l-o	45.5	6.7 ab	93.63 f-i
	W_{50}	5.2 m-r	1.2 i-l	1.7 g-j	2.6 g-j	4.4 gh	1.56 a-e	54.9	3.6 i-q	78.71 h-l
	W_{25}	4.6 o-r	1.1 j-l	1.2 h-j	1.8 i-o	3.0 g-k	1.45 a-g	39.0	2.3 q	47.35 p-s
Kuala Kencana	Control	30.0 a	4.5 a	9.1 a	5.3 a-c	14.4 a	0.58 l-o	48.6	4.5 e-l	138.46 bc
	W_L	22.2 d-h	4.2 ab	6.7 c-e	3.6 e-h	12.1 d-f	0.55 o	27.7	6.9 ab	90.73 g-j
	W_{50}	7.8 k-p	1.0 kl	1.5 h-j	1.7 i-o	3.2 g-k	1.14 b-l	29.1	2.8 n-q	66.03 k-p
	W_{25}	5.2 m-r	0.9 kl	1.1 h-j	1.4 j-o	2.5 g-k	1.21 b-l	26.6	2.4 pq	47.75 p-s
F-test :										
Treatment		476.55**	192.76**	303.60**	13.30**	260.82**	10.23**	20.85**	116.85**	374.59**
Population		26.48**	4.37**	21.34**	16.76**	23.96**	0.76ns	6.61**	4.68**	25.24**
Interaction		5.15**	3.36**	4.84**	2.6 *	4.19**	1.57 *	0.88ns	3.18**	2.33**

Remarks: SH=height increment, RCD=root collar diameter increment, ABG=above-ground biomass, BGB=below-ground biomass, TB=total biomass, R:S ratio = root-shoot ratio, RL = root length, NL = number of leaf, LA = leaf area. W_L = waterlogging, W_{50} = field capacity 50%, and W_{25} = field capacity 25%. Different letters within a column indicate significant differences at P < 0.05. ** = significant at 1%, *= significant at 5%, ns= non significant.

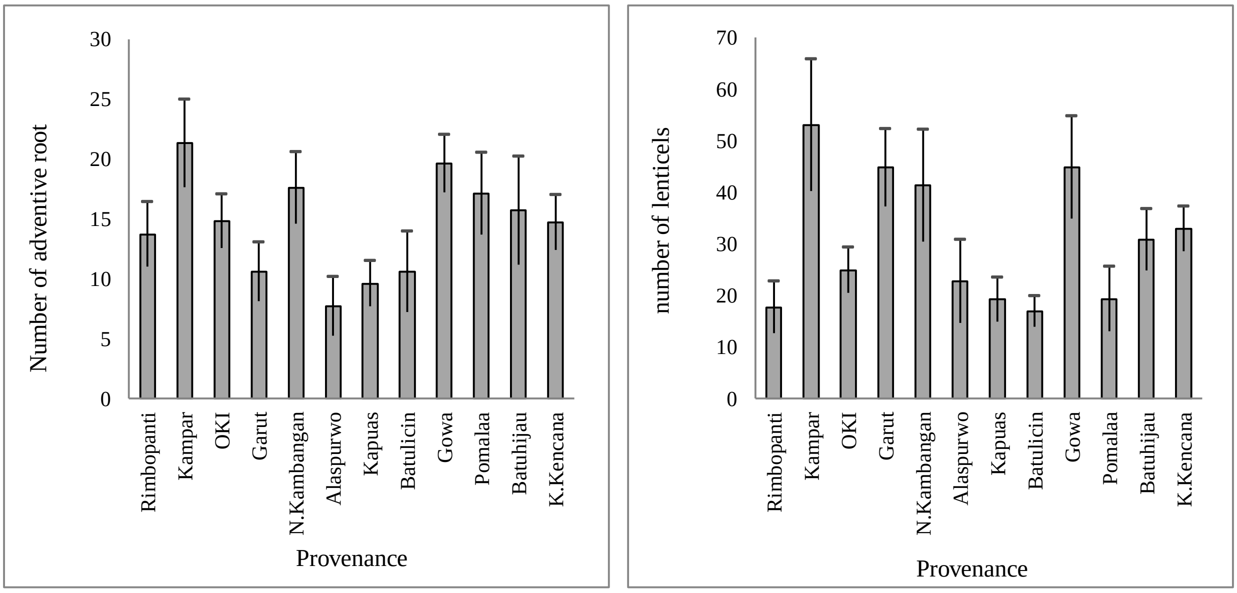

Figure 2. Number of adventive root and lenticels of each population in the waterlogging treatment

Specific Leaf Area, Relative Water Content and Leaf Thickness

Specific leaf area and relative water content was different for treatment and population, being highest in the W_L treatment and the lowest in the W_{25} treatment. Specific leaf area and relative water content are considered as measurement of water status, reflecting the metabolic activity in tissue and used as the most meaningful index for dehydration tolerance (Anjum *et al*., 2011). In the waterlogging treatment, Kampar population had the highest specific leaf area and relative water content, whereas in the drought (W_{25}) stress, Gowa population had the highest specific leaf area and relative water content (Table 3).

The leaf thickness had the trend to increase in response to water stress from the control, water logging, moderate drought (W_{50}) and severe drought stress (W_{25}) treatments. Plants growing in stress conditions usually have thicker leaves than those growing in wet conditions (Kofidis *et al*., 2004; Guerfel *et al*., 2009). Small and thicker leaves can withstand turgor pressure better than large and thinner leaves, and they can contribute to turgor maintenance more effectively under stress conditions. Gowa population had the thickest leaf and could be considered as a more adaptive population to drought stress.

Stomatal Density, Pigments and Proline Contents

Interaction of water stress treatment and population effects were significant for stomatal density that declined following the reduction of soil water content (Table 3). Most of the populations had the highest stomatal density in the W_L treatment, while the lowest stomatal density was shown by the W_{25} treatment. According to Sciutti and Morini (1995) concerning with air humidity, increased air humidity results in increased stomatal density. More stomata can take up more CO_2 and transpire more water. The mechanisms of water loss control through stomata (transpiration) seem to be an efficient process to maintain leaf turgor under drought condition. Gowa population had the lowest stomatal density in the drought stress (W_{25}) and transpired less water so more adaptive to drought stress.

The concentrations of chlorophyll A and chlorophyll B were initially different among populations. Increasing water stress, both drought and waterlogging significantly reduced the chlorophyll A and chlorophyll B. Conversely, carotenoids under severe drought tended to increase. The change in chlorophyll and carotenoids contents has been used to evaluate the influence of environmental stress on plant growth, and earlier study proved that chlorophyll contents usually decreased under drought (Singh and Reddy, 2011) and waterlogging stress (Xiaoling *et al*., 2011) due to their slow synthesis or fast breakdown (Amini *et al*., 2013; Sayyari *et al.,* 2013), instability of protein complexes and destruction of chlorophyll by increased activity of chlorophyll degrading enzymes and chlorophyllase under stress condition (Nunes *et al.,* 2008). On the other hand, the carotenoids contents tended to decrease under waterlogging and moderate drought (W_{50}) stresses, but slightly increase under severe drought stress (W_{25}). Increase of carotenoids content was also reported in drought stressed *Campylotropics polyantha* (Li *et al*., 2011). Carotenoids have essential functions in photosynthesis and photo-protection. Besides their structural roles, they are well known for their antioxidant activity, inhibiting lipid peroxidation and stabilizing membranes.

Proline content tended to increase both in waterlogging and drought stress. In the W_L treatment, proline content had higher than the one in other treatments. Most of populations in the W_L treatment were not significantly different in proline content, except for Rimbo Panti, OKI, Garut, and Nusa Kambangan populations which had relatively lower proline content (Table 3). This observation was similar with Ibrahim (2013) who reported significant increase of proline in leaves of waterlogged seedlings. In this study, the proline content increased under moderate drought (W_{50}) and then decreased under severe drought stress (W_{25}). A decrease in proline in severe drought soil is usually correlated to lower drought tolerance in white jabon seedlings. Many authors reported the significant relation of proline content with water deficit (Cordeiro *et al*., 2009; Singh and Reddy, 2011). Proline has important roles in osmosis balance and plays a highly protective role in plants that are subjected to abiotic stresses. It has been also proven that proline has an essential role in stabilizing proteins and cellular membranes in plant cells in the presence of high levels of osmolytes (Farooq *et al*., 2009).

Table 3. Specific leaf area, relative water content, leaf thickness, stomatal density, pigments, and proline contents of white jabon seedling under four water treatments

Population	Treatment	SLA (cm^2/g)	RWC (%)	LT (µm)	SD (number /mm^2)	Chl A (mg/g)	Chl B (mg/g)	Tot. Chl (mg/g)	Car. (mg/g)	Pro (µg/g FM)
Rimbo Panti	Control	190.39 j-p	74.5 a-m	116.7 s-u	467.09 g-o	1.32 bc	0.55 bc	1.87	0.29 d-k	0.023 k-n
	W_L	305.32 a-d	84.6 a-c	150.5 i-o	579.19 a-e	0.64 m-r	0.32 h-p	0.96	0.22 Kl	0.108 b
	W_{50}	160.45 m-q	65.9 k-q	176.1 bc	520.59 b-i	0.83 h-n	0.33 g-p	1.16	0.28 e-l	0.045 e-l
	W_{25}	144.49 pq	59.1 p-t	149.9 j-o	403.40 m-q	0.53 r	0.26 k-p	0.79	0.41 Bc	0.051 e-i
Kampar	Control	212.05 g-n	83.6 a-d	140.5 n-q	470.49 g-o	1.16 b-f	0.49 b-e	1.66	0.28 e-l	0.027 h-n
	W_L	327.44 a	85.7 a	160.4 e-l	518.05 b-j	0.81 h-o	0.34 g-p	1.15	0.19 l	0.142 a
	W_{50}	180.35 k-q	68.0 h-q	183.5 ab	480.68 f-j	0.55 p-r	0.38 d-m	0.76	0.24 h-l	0.060 d-f
	W_{25}	163.80 l-q	56.1 q-s	153.2 h-n	408.49 l-q	0.52 r	0.22 op	0.74	0.36 c-f	0.041 e-m
OKI	Control	195.64 i-p	80.2 a-h	128.6 q-s	421.23 i-q	1.34 b	0.53 bc	1.87	0.34 c-h	0.024 j-n
	W_L	265.00 c-g	82.3 a-e	139.8 o-q	417.84 j-q	0.89 g-l	0.29 i-p	1.28	0.34 c-h	0.109 b
	W_{50}	171.74 k-q	68.0 i-q	165.5 c-h	388.18 o-q	0.85 h-m	0.34 f-p	1.21	0.28 e-l	0.055 ef
	W_{25}	159.44 m-q	62.8 m-s	141.5 n-p	417.84 j-q	0.68 k-r	0.21 p	1.04	0.42 bc	0.026 i-n
Garut	Control	188.75 j-q	76.6 a-l	103.1 v	518.05 b-j	1.09 c-g	0.45 b-h	1.53	0.28 e-l	0.020 l-n
	W_L	321.86 ab	82.2 a-e	167.6 c-g	577.49 a-f	0.78 i-q	0.33 g-p	1.11	0.27 f-l	0.051 l-i
	W_{50}	179.96 k-q	66.5 j-q	193.9 a	469.64 g-o	0.73 j-r	0.31 i-p	1.05	0.24 h-l	0.022 k-n
	W_{25}	130.13 q	61.7 n-s	125.0 r-t	495.12 d-n	0.66 l-r	0.26 l-p	0.92	0.37 c-f	0.025 i-n
Nusa Kambangan	Control	197.58 h-p	77.7 a-k	117.7 s-u	473.89 g-o	1.61 a	0.73 a	2.33	0.28 e-l	0.015 n
	W_L	295.39 a-e	78.2 a-j	148.8 k-o	574.95 a-f	1.17 b-f	0.46 b-g	1.63	0.41 bc	0.107 b
	W_{50}	177.63 k-q	69.7 f-p	156.7 g-m	469.64 g-o	0.99 e-i	0.39 d-k	1.39	0.27 f-l	0.053 e-g
	W_{25}	149.85 o-q	64.8 i-r	144.7 m-o	461.15 g-p	0.71 j-r	0.31 i-p	0.80	0.53 a	0.047 e-k
Alas Purwo	Control	185.10 j-q	74.7 a-m	113.7 t-v	421.23 i-q	1.24 b-d	0.51 b-d	1.76	0.25 h-l	0.053 e-h
	W_L	295.39 a-e	80.3 a-g	165.6 c-h	656.48 a	0.67 l-r	0.26 k-p	0.94	0.20 k-l	0.133 b
	W_{50}	166.01 l-q	68.7 g-o	155.6 g-m	480.68 e-o	0.73 j-r	0.30 i-p	1.03	0.27 f-l	0.028 g-n
	W_{25}	158.15 n-q	56.6 q-t	160.8 e-l	365.18 o-q	0.52 r	0.23 op	0.74	0.40 bc	0.080 c-d

Table 3. *(Continued)*

Population	**Treatment**	**SLA (cm^2/g)**	**RWC (%)**	**LT (µm)**	**SD (number/ mm^2)**	**Chl A (mg/g)**	**Chl B (mg/g)**	**Tot. Chl (mg/g)**	**Car. (mg/g)**	**Pro (µg/g FM)**
Kapuas	Control	197.33 h-p	72.6 c-o	123.9 r-u	517.20 b-j	1.27 bc	0.54 bc	1.81	0.27 f-l	0.025 i-n
	W_L	276.28 a-f	75.1 a-m	181.4 b	585.14 a-d	0.59 n-r	0.26 l-p	0.85	0.23 i-l	0.137 a
	W_{50}	159.89 m-q	61.2 o-s	120.8 r-u	412.74 k-q	0.89 g-l	0.43 b-i	1.31	0.32 c-j	0.014 n
	W_{25}	130.13 q	48.1 t	155.2 g-m	469.64 g-o	0.57 o-r	0.24 n-p	0.81	0.46 ab	0.016 mn
Batu Licin	Control	204.51 h-o	78.8 a-i	111.4 u-v	433.97 i-q	1.15 b-f	0.48 b-f	1.63	0.24 h-l	0.051 e-i
	W_L	251.74 d-i	79.1 a-i	175.8 b-d	489.17 d-o	1.03 d-h	0.43 c-j	1.46	0.35 c-g	0.142 A
	W_{50}	159.20 m-q	66.9 i-q	128.9 p-s	406.80 l-q	0.94 f-j	0.39 d-k	1.33	0.32 c-j	0.024 j-n
	W_{25}	140.88 pq	49.4 t	128.3 q-s	396.60 m-q	0.62 m-r	0.25 m-p	0.88	0.38 b-d	0.012 N
Gowa	Control	185.10 j-q	82.3 a-e	151.1 i-o	517.20 b-j	1.20 b-e	0.56 b	1.76	0.27 f-l	0.027 h-n
	W_L	312.80 a-c	85.5 ab	160.7 e-l	597.88 a-c	0.68 k-r	0.30 i-p	0.97	0.25 h-l	0.150 A
	W_{50}	197.70 h-p	72.0 d-o	176.5 bc	577.49 a-f	0.81 h-o	0.32 h-p	1.13	0.24 h-l	0.090 bc
	W_{25}	182.98 j-q	67.7 i-q	172.5 b-e	496.82 d-m	0.65 m-r	0.28 k-p	0.93	0.39 b-d	0.093 bc
Pomalaa	Control	220.78 f-l	81.0 a-f	123.1 r-u	439.07 h-q	1.39 b	0.54 bc	1.92	0.37 b-e	0.062 de
	W_L	230.39 f-k	83.2 a-e	162.9 d-j	605.52 ab	0.95 f-j	0.39 d-k	1.35	0.22 kl	0.145 A
	W_{50}	202.17 h-o	71.1 e-p	161.0 e-l	479.83 f-o	0.85 h-m	0.35 f-o	1.20	0.28 e-l	0.097 bc
	W_{25}	148.18 o-q	67.7 i-q	140.0 n-q	436.73 k-q	0.69 k-r	0.28 k-p	0.97	0.41 bc	0.090 bc
Batu Hijau	Control	175.56 k-q	73.8 b-n	147.8 l-o	509.56 b-j	1.29 bc	0.54 bc	1.83	0.33 c-i	0.053 e-h
	W_L	267.27 b-g	77.6 a-k	170.9 b-f	540.13 b-g	0.91 g-l	0.37 e-n	1.28	0.26 g-l	0.149 a
	W_{50}	161.37 l-q	71.4 d-o	161.6 e-k	395.76 n-q	0.92 g-k	0.36 e-n	1.28	0.32 c-j	0.036 e-n
	W_{25}	147.93 o-q	53.8 r-t	163.8 c-i	352.44 q	0.66 l-r	0.27 k-p	0.93	0.40 bc	0.087 bc
Kuala Kencana	Control	219.17 g-l	73.3 b-o	131.3 p-r	505.31 c-k	1.38 b	0.51 b-d	1.74	0.33 c-i	0.048 e-k
	W_L	286.78 a-e	84.6 a-c	158.5 f-l	536.73 b-h	0.72 j-r	0.31 i-p	1.02	0.28 e-l	0.158 a
	W_{50}	159.89 m-q	72.0 d-o	165.7 c-h	512.10 b-k	0.79 h-p	0.34 g-p	1.12	0.26 g-l	0.035 f-n
	W_{25}	168.25 l-q	52.2 st	154.7 g-m	469.64 g-o	0.52 qr	0.29 j-p	0.84	0.39 b-d	0.049 e-j
F-test :										
Treatment		115.19 **	85.72 **	222.35 **	34.92 **	187.87**	04.90**	4.14**	62.27**	356.86**
Population		2.22 *	3.65 **	18.01 **	6.89 **	7.76**	4.36**	0.82ns	5.70**	24.70**
Interaction		2.25 *	2.41 *	14.77 **	3.14 **	1.83 *	2.35 *	0.77ns	2.80 *	6.79**

Remarks: SLA=specific leaf area, RWC=relative water content, LT=leaf thickness, SD = stomatal density, Chl A = chlorophyll A, Chl B = chlorophyll B, Tot Chl = total chlorophyll, Car = carotenoids, Pro = proline. W_L = waterlogging, W_{50} = field capacity 50%, and W_{25} = field capacity 25%. Different letters within the column indicate significant differences at $P < 0.05$. ** = significant at 1%, *= significant at 5%, ns= non significant.

Table 4. Evaluation of tolerance indices of 12 white jabon populations to drought and waterlogging stress

Population	Treatments								
	Waterlogging			50% field capacity			25% field capacity		
	SH	RCD	TB	SH	RCD	TB	SH	RCD	TB
Rimbo Panti	0.95	0.82	1.04	**0.48**	**0.27**	**0.34**	**0.24**	**0.17**	**0.29**
Kampar	**1.29**	**1.29**	**1.32**	**0.40**	**0.42**	**0.38**	**0.26**	**0.27**	**0.29**
OKI	**1.14**	**1.21**	**1.22**	0.41	0.29	0.36	0.20	0.28	0.16
Garut	0.48	0.95	1.04	0.23	0.23	0.42	0.11	0.19	0.30
Nusa Kambangan	1.01	1.38	0.51	0.44	0.37	0.22	0.19	0.28	0.19
Alas Purwo	0.43	0.99	0.32	0.23	0.28	0.20	0.13	0.15	0.17
Kapuas	0.16	0.76	0.11	0.07	0.23	0.04	0.05	0.17	0.03
Batu Hijau	0.14	0.61	0.09	0.06	0.18	0.04	0.05	0.15	0.02
Gowa	**1.12**	**1.71**	**1.27**	**0.49**	**0.66**	**0.55**	**0.41**	**0.35**	**0.45**
Pomalaa	0.77	1.23	1.30	**0.29**	**0.39**	**0.34**	**0.20**	**0.23**	**0.30**
Batu Hijau	0.82	1.37	1.22	0.22	0.32	0.44	0.19	0.29	0.30
Kuala Kencana	**1.25**	**1.74**	**1.00**	0.47	0.29	0.32	0.31	0.26	0.25

Remarks: SH= seedling height, RCD=root collar diameter, TB=total biomass.

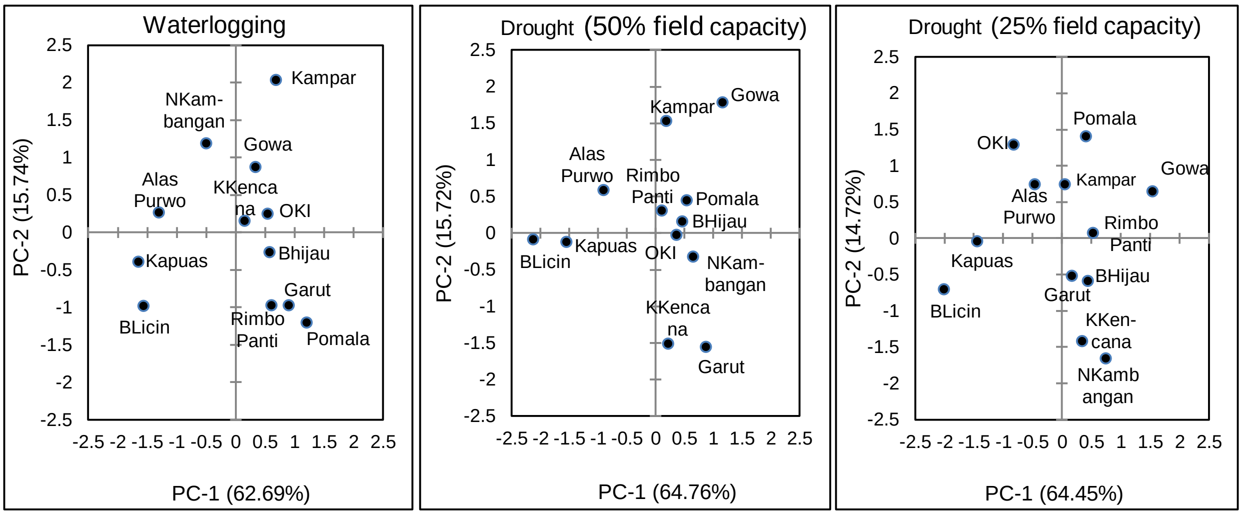

Figure 3. Biplot of seedling adaptability of white jabon from 12 populations to drought and waterlogging based on seedling morphophysiological characteristics

Stress Tolerance Index and Clustering of Population Adaptability

Population with high stress tolerance index (STI) had better adaptability to stress. The highest STI in the WL treatment was indicated by Kampar population (seedling height and total biomass) and Kuala Kencana population (root collar diameter). In the W_{50} and W_{25} treatments, Gowa population had the highest STI. Kampar population had the highest STI in height and total biomass (Table 4). STI can be used to identify genotypes that produce high growth and biomass under both stress and non-stress conditions (Fernandez, 1992) so the higher STI showed the better adaptability of the genotype (Olaoye *et al*., 2009). Gowa population had highest STI in height, root collar diameter and total biomass indicating Gowa population was more adaptive to drought stress than the other populations.

The trend of STI is similar with biplot graphical of principal component analysis for clustering of seedling adaptation. Some populations were identified more tolerant to waterlogging stress such as Kampar, Gowa, Kuala Kencana and OKI. Based on STI, all of the white jabon population is not tolerant to drought stress, and more adaptive to waterlogging. Adaptability of white jabon seedlings to waterlogging is correlated with natural habitats of jabon, generally distributed on the deep, moist, and alluvial sites and vice versa, the general condition of the natural habitat also affected the adaptation of seedlings that is less adapted to drought stress. However considering the seedling growth, survival and biplot from principal component analysis, some populations were more adaptive to drought stress, i.e. Gowa, Pomalaa, and Kampar populations. The identified populations are more potential to be transferred and planted in the marginal sites especially in drought and waterlogged areas.

CONCLUSION

White jabon seedlings were more tolerant to waterlogging than drought stress, which can be observed from morphological, physiological and anatomical traits, and the absence of seedling under the waterlogging treatment that died during the experiment. In order to cope with water stress, the following was conducted by avoidance mechanism achieved through morphological changes (leaf morphology, adventives root, lenticels) and also by tolerance mechanism achieved by cell and tissue specific physiology, biochemistry (chlorophyll and carotenoids), and accumulation of proline. From several indicators of morphology, physiology, and biochemistry, Kampar, Gowa, Kuala Kencana, and OKI populations were indicated as the populations which were able to be well adapted to the waterlogging stress, and the populations can be used for rehabilitation activities of waterlogged marginal sites. In the drought stress, Gowa, Pomalaa, and Kampar populations had relatively better performance than the other populations, and the populations can be used for replanting the dryer marginal sites.

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